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THE AMERICAN PATROBINI (COLEOPTERA, CARABIDAE)

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Introduction and Acknowledgments

This paper is intended to revise the American genera and species of the Carabid tribe Patrobini, a group badly in need of revision as a result of the arch-conservatism of George Horn and the vile "Observations" of T. L. Casey, and then to utilize taxonomic and other data to reconstruct, so far as possible, the history of the species of Patrobus in America. Coleopterists are so far from agreement on the conceptions and methods underlying taxonomy, however, that a good deal of discussion of generalities is necessary before the real work of the paper can be begun.

The material I have used is, first, that in the Museum of Comparative Zoölogy, Harvard University. This includes Leconte's types; probable cotypes of several species received by Leconte from Eschscholtz, Mannerheim, and Motschulsky; and series from Labrador (Asa S. Packard and Samuel Henshaw) and Newfoundland (Percy Gardner Bolster). During the course of the work I have visited the United States National Museum, which contains the Casey Collection as well as much other material; the American Museum of Natural History; and the Philadelphia Academy of Sciences, which contains the George Horn Collection. I have borrowed material for further study from some of these institutions and from the California Academy of Sciences, the Canadian National Collection, and the University of Kansas, as well as from Mr. John Carr (collection of F. S. Carr), Dr. H. C. Fall, Mr. C. A. Frost, Dr. M. H. Hatch, Mr. Ralph Hopping, Mr. H. B. Leech, Mr. Howard Notman, Mr. J. B. Wallis, Mr. G. Stace Smith, and Miss Edith Mank. I am indebted also, for various favors, to Dr. E. C. Van Dyke, Dr. Walther Horn, Mr. W. J. Brown, Mr. L. L. Buchanan, Mr. H. P. Löding, Mr. M. W. Sanderson, and Dr. F. M. Carpenter. I have used, also, material from my own collection, including Labrador specimens given me by Mr. John D. Sherman, Jr. pean Patrobus have been received by exchange from Dr. Carl H. Lindroth and Dr. Walther Horn, and other Old World species have been purchased from Staudinger and Bang-Haas.

NOMENCLATORIAL UNITS

The criteria which I have used to decide whether given forms should be called *species* or *subspecies*, in cases where morphological differences are not decisive, are these: two closely allied forms are species if their ranges overlap without definite intergradation (*Platidius aterrimus* and *filicornis*, Pl. 4, map A); subspecies, if their

ranges are complementary or nearly so, especially if there is intergradation at the boundary (Patrobus fossifrons dimorphicus and P. f. stygicus; see discussion under latter), or if the two forms occupy similar but discontinuous habitats and are unquestionably slightly modified forms of a single original stock, even if their ranges are not in contact and if no intergradation occurs (Thalassotrechus barbarae barbarae and T. b. nigripennis, footnote 3). These criteria work reasonably well, although there is room for differences of opinion in some cases. They make the subspecies a purely geographical concept, usage which is becoming more or less standardized in zoölogy. Non-geographical variations, often called varieties or aberrations, are here regarded as not worth special names, by which. of course, I do not mean that they are not worth study. Too many coleopterists make no distinction between what is worth examining and recording and what is worth naming. The Patrobini, like many other boreal Carabidae, are often extremely variable individually. so that it is necessary to be conservative in making subspecies. In certain species there are minor, average, inconstant differences which distinguish series from nearly every different locality. Such local resemblances are probably of about the same significance as family resemblances among human beings. To attempt to distinguish and name such indefinite forms (as Casev tried to do) would lead to endless confusion. Sometimes, too, species show slight, continuous geographical variation in certain structures (e.g., the development of the tooth near the apex of the phallobase in males of Patrobus longicornis), but I do not believe that this justifies a division into subspecies unless there is a distinct break in the range of variation.

Subgenera can probably be usefully employed in several ways. They may be geographical, like subspecies; i.e., groups of species inhabiting different geographical areas may conveniently be treated as subgenera if the groups are natural but not distinct enough to stand as full genera. Subgeneric names may profitably be used, too, to designate poorly defined but natural groups of species in large genera which would otherwise be unwieldy. Or subgenera may be used, as in *Patrobus* in this paper, to emphasize important phylogenetic relationships.

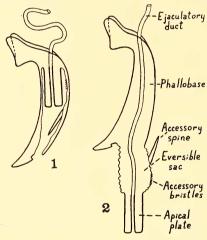
On the other hand, it seems to me that neither the subspecies nor the subgenus should be used, as they sometimes are, merely to desig-

¹ This is perhaps the result of alternate periods of isolation and mixing of poorly defined local forms in the north, during and immediately following successive Pleistocene glaciations.

nate groups about which an author is doubtful or ignorant. The description of these categories should require more rather than less knowledge than the description of full species and full genera, for to describe the latter it is not absolutely necessary to know more than that they are different from previously described forms, while the proper description of subspecies and subgenera requires a thorough knowledge of relationship and of difference. Properly employed, the concepts of subspecies and subgenus are very useful, but, if they are improperly used, they are likely to make an already confusing system of taxonomy still more confusing.

GENITALIA

The male copulatory organs of Patrobini, as usual among Carabidae, consist of a median lobe and a pair of lateral lobes or parameres.



Text Figs. 1 & 2. Diagrams of middle lobe of male genitalia of *Patrobus*, from left. Fig. 1, with eversible sac retracted as it usually is in museum specimens; fig. 2, with eversible sac extended.

The median lobe (Text figs. 1 and 2) is derived from a single continuous tube which is, however, modified to form a basal piece or phallobase (called also the tegmen), an eversible sac, and an ejaculatory duet.

The phallobase is an asymmetrical, strongly chitinized, troughlike or tube-like organ with a hook-shaped base. It is open pos-

teriorly and dorsally, or the sides may overlap dorsally, but without fusing. In repose, the phallobase lies on its right side in the abdomen; at such times it contains and protects the delicate eversible sac. During copulation the phallobase is exserted and performs the first entry into the abdomen of the female. The hooked basal portion of the phallobase then serves to hold the tip of the abdomen of the male securely to that of the female while the sac is everted through the apical trough- or tube-like portion. The function of the phallobase is, therefore, that of an anchor and protective easing through which more delicate organs perform insemination.

The eversible sac is extremely variable even in the single tribe Patrobini, but some part of it is always so lightly chitinized that it can be reversed like the finger of a glove as the sac is drawn out of or back into the phallobase. Rarely the sac is simple and little differentiated (Patroboidea), more commonly it is divided into a soft eversible portion and a chitinized apical spine or plate. The eversible portion may be divided in turn into a less and a slightly more chitinized (but still pliable) part, and the latter may be provided with many small bristles (*Platidius*), or the sac may be provided with one or two conspicuous accessory spines and sometimes with special, pigmented, localized patches of bristles (Patrobus). Text figs. 1 and 2 for diagrams; Pl. 1, figs. 1-4 for drawings of eversible sacs of *Platidius* and *Patrobus*.) The accessory spines and bristles are, I think, invariably adaptations to aid in the folding and unfolding of the sac. I have not studied the muscles of the copulatory organs, but it is obvious that the sac is everted chiefly by fluid pressure, not by muscles. The accessory spines, which emerge from the phallobase point first and then turn backwards, must act as levers aiding both the drawing out and, later, the refolding of the sac into the phallobase. They probably tend to prevent the sac from crumpling irregularly, as a simple sac operated partly by fluid pressure might do. The areas of bristles are probably creeping organs which help to carry the unfolding sac into the vaginal cavity of the female and which may help also in orderly refolding.

The apical plate of the eversible sac may be simple and spine-like (*Platidius*) or very complex (*Patrobus*). Through its base, but not always through its whole length, the sperm is actually discharged, and it is sometimes, therefore, called the "transfer apparatus." However, this is probably not a good term, for it implies more than is really known about the organ's function. Its primary function is probably that of an apodeme which strengthens the eversible sac at the point where the ejaculatory duct is attached, and which may

serve also as an attachment for retracting muscles. In some Patrobini I think the apical plate has, for one of its functions, merely to simplify the folding and unfolding of the eversible sac. A mechanism consisting of two telescoping tubes (phallobase and apical plate of Patrobus) connected by a membrane is probably much simpler in operation than a single tube into and out of which a voluminous undifferentiated sac must be forced partly by fluid pressure. This is more than a guess. I have found it much easier artificially to evert sacs with well developed than with poorly developed apical spines or plates. For example, it is easier to push out with a blunt pin the sac of Platidius aterrimus, which has a stiff apical spine, than of P. filicornis, in which the apical spine is membranous, and the sac of Patrobus foveocollis, which has an enormous apical plate, is the easiest of any of the Patrobus to evert.

The ejaculatory duct is a slender tube running from the testes through the phallobase and eversible sac, and attached to the apex of the latter, to the base of the apical plate or spine if one is present, so that the duct is drawn out when the sac is everted. The duct, of course, actually carries the sperm; all the other parts of the copulatory apparatus serve merely to draw out the duct and later to return it to its place in the male abdomen.

The lateral lobes or parameres of the male copulatory organs articulate with the base of the phallobase (left paramere outlined in Pl. 1, fig. 6; Pl. 2, figs. 18, 28, 38; Pl. 3, figs. 55, 70, 77). In the Patrobini the right and left parameres are approximately equal. They are tipped with setae, and are probably tactile organs.

In the female there are three pairs of retractile, chitinized plates at the tip of the abdomen. These are often called the female genitalia, but functionally they are probably as much concerned with excretion, oviposition, and other activities involving the tip of the abdomen as with copulation. It is better to call them retractile plates than genitalia. The latter name should probably be reserved for the vaginal cavity, the ovaries, and the other parts of the true genital system. The latter sometimes is not even mentioned in papers on "female genitalia"!

The male copulatory organs are extremely useful in taxonomy of Patrobini. The form of the apex of the phallobase, beyond the subapical orifice, yields useful specific characters. The position and form of the plates and spines of the eversible sac frequently distinguish species and genera, and are particularly useful in showing true relationships among groups of superficially similar species. Details of the phallobase and eversible sac are often too unstable to

be used in classification of higher categories, but the parameres are more stable and yield tribal as well as generic characters. There are slight and inconstant differences also in the form of the retractile plates of female Patrobus of different species, but the differences are of little practical use and add nothing to our knowledge of phylogeny. There are variations also in the structure of the vaginal cavity of different Patrobus. These variations seem to be somewhat correlated with the form of the apical plate of the male copulatory organs, but it is difficult to make proper dissections, and the females can be identified better by other characters.

It should be noted that there is often great variability in the genitalia of single species of Patrobini. The variation is both individual and geographic, and occurs in both sexes. For this reason genitalic characters in the Patrobini must be tested as carefully as any other characters, by examination of series of specimens and correlation with other structures.²

INNER WINGS

Recently (1936) I have described the variation of the wings of certain Carabidae and the correlations which usually exist between the state of the wings and the habitat of the insects. The wings of different American Patrobini range from a uniformly full, through dimorphic, to a uniformly vestigial condition, and the correlation between the state of the wings and the habitat of the insects is about as described in the paper cited. The majority of the species (those of Patroboidea, Platypatrobus, and Platidius, and Patrobus septen-

² The very fact that striking genitalic characters so often distinguish otherwise similar species of insects suggests that the genitalia are more variable than other parts of the body, for rapid evolution of differences practically requires great individual variation. some cases the variation can be seen in nature. For example, in Platidius aterrimus the apex of the phallobase of the male genitalia (Pl. 3, figs. 89-92) is more variable than any other part of the insect. It seems probable that the genitalia of insects, like their wings, may sometimes undergo mutation and dimorphism, and that two or more distinct forms of genitalia may exist in one species at one time and place. The difference in form of the apex of the phallobase in Patrobus fossifrons dimorphicus and P. f. stygicus (see discussion under latter) is very suggestive of mutation and dimorphism overlain by a certain amount of other variation. It would be interesting to see certain recent taxonomic papers reviewed with the possibility of mutation and dimorphism in mind.

trionis) are probably always fully winged and capable of flight, and are probably all strictly riparian hydrophiles, except that *Patrobus* septentrionis is merely a facultative hydrophile, and that the habits of Platypatrobus are unknown. The wings of the remaining American species of *Patrobus* are dimorphic, but not uniformly so. *Patro*bus longicornis is probably dimorphic throughout its entire range. Typical lecontei of north-central North America is dimorphic, too, but its subspecies aravidus of Newfoundland has the wings uniformly vestigial in the small series seen. The three subspecies of *Patrobus* fossifrons show the whole range from uniformly vestigial (typical fossifrons of islands off Alaska), through dimorphic (subspecies dimorphicus of western continental regions), to uniformly full wings (subspecies stygicus of central and eastern boreal America). Finally Patrobus foveocollis of the Aleutian Islands, and its North American subspecies tenuis, have uniformly vestigial wings, but a subspecies from islands off Kamchatka has the wings uniformly full, although it is otherwise indistinguishable from tenuis. All the American species of *Patrobus* are less strict hydrophiles than the fully winged genera of Patrobini, but they are still facultative hydrophiles, except that foveocollis, the only species which is always flightless in America. seems to have become a more or less strict mesophile.

ISLAND FORMS

There is an obvious tendency for several species of *Patrobus* to develop large insular subspecies on the islands of Unalaska and Newfoundland. This might be an interesting subject for special study. The state of the wings in some insular *Patrobus* is of interest, too. I have been accumulating data on the wings of mountain and island Carabidae for several years, and hope eventually to publish a paper on the subject.

Geographical Distribution

Most American Patrobini have moderately wide or very wide ranges. In mapping them (Plates 4 & 5) I have shown not only specific localities, but the approximate gross ranges of the species, to enable the reader to appreciate more easily both the extent of different ranges and their interrelationship. It must not be forgotten that the gross ranges are only approximate. It should be remembered especially that I have seen very little material from the far north between the coast of Labrador and that of southern Alaska, so that the northern limit of range of the arctic species is almost unknown.

If the maps are looked at obliquely from the direction of the lines which mark any given range, it will be found that that range will stand out more sharply than the others.

Methods

My descriptions have been drawn from small series of each species, selected to show extremes of variation, but important characters have been checked in all material. All relative proportions of parts of the body (e.g., the width of the head in relation to the prothorax) have been determined by actual measurements made with a ruled ocular in a binocular microscope. As for the male copulatory organs, the tip of the phallobase is often sufficiently exerted for identification in ordinary museum specimens. When not, the specimens have been relaxed, the abdomens removed, and the copulatory organs dissected out from above. Both the organs and the abdomens have usually then been mounted with shellac on points under the specimens. This has the advantage of allowing the state of the inner wings to be seen from below. Genitalia to be dissected or everted or drawn in detail have been softened in 10% caustic potash (half an hour or more, cold), manipulated in alcohol, drawn in alcohol or xylol, and finally mounted on slides.

The references cited under the different species do not include incidental references or records from faunal lists. So many of the species of *Patrobus* (except *longicornis*) have been misidentified in the past that most published records are worthless.

The tribe Pogonini of Horn (1881, p. 135) and others, which is the same as the Trechini of Sloane (1923, p. 245), is unnatural and must be divided into three groups, each of which is usually now called a tribe. The American representatives of the three may be separated as follows:

KEY TO TRIBES

- Frontal foveae not extending behind eyes; ligula 2-setose............ 2

³ Besides *Pogonus*, *Pogonistes*, and *Diplochaetus*, *Thalassotrechus* goes in the Pogonini, as might be inferred from Van Dyke's (1918,

The tribe Patrobini as thus defined is equivalent to the Patrobidae of Chaudoir (1871, p. 39).

I am not prepared to discuss the affinities of the Patrobini, except to say that they are probably with some group of the Pterostichini rather than with the true Trechini.

pp. 303–304) discussion, although Horn first described barbarae as a species of Trechus. Thalassotrechus is not Pogonus-like in appearance, it lacks the internal elytral plica of typical Pogonini (notwithstanding Horn's and Sloane's classifications, Pogonus and its allies and *Patrobus* and its allies have this plica well developed). and it has the hind coxae slightly separated. However, these anomalies are probably merely the natural results of the adaptation of Thalassotrechus to an intertidal habitat. The inner wings of the insect have atrophied, as they have in so many seaside beetles; the metathorax has been reduced as a consequence of the loss of the wing muscles; and the elytra have at the same time been narrowed across the humeri, the narrowing being accompanied by a coaptive narrowing of the base of the prothorax. All this has resulted in a change from a *Pogonus*-like to a *Trechus*-like form. The change in shape of the metathorax may well have resulted in the slight change which has occurred in its relation to the hind coxae. the loss of the elytral plica may conceivably be due to a change or partial loss of function of the elytra following the atrophy of the wings. The of genitalia of Thalassotrechus (Pl. 1, fig. 5) are definitely of the *Pogonus* type.

Since I have had series of both known forms of *Thalassotrechus* for study, I give the following notes on their taxonomy. The two are best considered subspecies. *T. barbarae barbarae* (Horn) was described from Santa Barbara, California, and was rediscovered there a few years ago by the late Dr. J. G. Gehring. *T. barbarae nigripennis* Van Dyke, of which Dr. Van Dyke has very kindly supplied me with topotypes, was described from Moss Beach, just south of San Francisco, California, and is known from two or three other localities in the San Francisco region, which is about 300 miles by coast north of Santa Barbara. It is a very distinct subspecies, differing from typical *barbarae* in having the elytra duller and black rather than rufo-testaceous or castaneous. There is no constant difference in width of prothorax, but the anterior angles of the latter are minutely more flattened and more prominent in *barbarae* than in *nigripennis*. The A genitalia of the two are not distinguishable.

Key to American Genera of Patrobini4

- 1. Elytra each with numerous dorsal setigerous punctures on third interval, with additional punctures basally on first and fifth intervals; (male unknown).....2. Platypatrobus gen. n.
- Each elytron with 3 (rarely 4) dorsal setigerous punctures on third stria or outer edge third interval
- 2. Palpi with apical segments subconical; genae longer than eyes; total length of insect less than 6 mm.; (& genitalia with apices of parameres relatively short; phallobase open above; eversible sac without distinct apical plate or spine).

1. Patroboidea Van Dyke

- More convex; occipital constriction deep; basal foveae of pronotum deep; middle groove of pronotum very coarse basally; mesosternal epimera narrow; (eversible sac with complex apical plate and 1 or 2 accessory spines).

4. Patrobus Dei.

1. Patroboidea Van Dyke

Van Dyke 1925, p. 67.

Genotype: Patroboidea rufa Van Dyke (Pl. 1, figs. 6-8) Van

Dyke 1925, p. 69.

There is no point in repeating Dr. Van Dyke's recent good descriptions of genus and species. The male genitalia are like those of other Patrobini but with parameres only briefly produced at apex, sides of phallobase not meeting above, and eversible sac without dis-

⁴ Dr. Hatch (1935, p. 118) has recently pointed out that his *Monillipatrobus* is a synonym of *Psydrus*. This genus probably belongs with the primitive Pterostichini, but is not very closely related to the Patrobini. The δ genitalia of *Psydrus* have the parameres symmetrical but are otherwise unlike those of the Patrobini. A proper understanding of the relationships of the Pterostichini and related groups would require an enormous amount of study and dissection, especially of exotic genera.

tinct apical plate or accessory spines, but apparently with several strong, parallel bristles near base.

Type: From Monroe, Washington State (California Acad. Sci.)

(not seen by me).

Distribution: I have seen specimens from Stanley and Spious Creek, B. C. (the latter Van Dyke's paratype, now in the Canadian Nat. Coll.; the former received for the M. C. Z. through the kindness of Mr. Ralph Hopping) and Ft. Yukon, Alaska (Coll. H. C. Fall). The species seems to be rare everywhere. It is found under cover by streams.

2. Platypatrobus gen. n.

A typical member of the Patrobini (= Patrobidae) as characterized by Chaudoir (1871, p. 39). Characterized within the tribe by rather depressed form; excessively prominent eyes; genae very short, with deep basal constriction of head immediately behind eyes; vertex and sides of head not hairy; frontal sulci well impressed; apical segments of palpi subcylindrical and subtruncate; prothorax with side margins plurisetose, basal foveae deep, middle groove very coarse basally; elytra with numerous setigerous punctures on intervals 1, 3, and 5; mesosternum plurisetose between coxae, with epimera moderately broadly triangular; appendages slender (general structure as in *Patrobus*); tarsi not hairy above, 4th segment of two anterior pair moderately broad, emarginate.

This genus does not fit very well into any of the subtribal groups proposed by Chaudoir (l. c.). The form and appearance are very Nebria-like. The extra setae of margins of prothorax and of the mesosternal process suggest the European genus Deltomerus, but in the latter the eyes are very much less prominent, much removed from the basal constriction of the head, and the vertex and sides of head are hairy. The new genus resembles Patrobus but is more depressed, with more prominent eyes, with more setae on thoracic margins, elytral intervals, and mesosternum, and with broader mesosternal epimera. Until the male is found and the copulatory organs examined it is useless to guess at the true relationships of the new genus.

GENOTYPE: Platypatrobus lacustris sp. n. (Pl. 1, fig. 9).

Form as figured, rather broad, depressed; dark rufous; appendages slender, rufo-testaceous; head and prothorax shining, elytra finely alutaceous. $Head_{0} = 0$ width prothorax; eyes very prominent; frontal sulci well impressed, not punctate,

curved outward posteriorly, ending about opposite middle of eves: front not transversely impressed: basal constriction deep. slightly punctate; antennae with 3rd segment between 3 and 4 times long as wide; maxillary palpi with apical segment \(\frac{1}{4} \) longer than subapical; sides of neck below punctate; gular puncture weak. Prothorax cordate, not quite \frac{1}{2} wider than long; sides arcuate anteriorly, strongly sinuate before right posterior angles; latter weakly carinate; side margins moderate, left with 4, right with 3 setae before middle, and each with seta at basal angle; basal foveae slightly punctate; anterior transverse impression moderate but not well defined posteriorly. with a few coarse punctures. Elytra not quite $\frac{2}{3}$ wider than prothorax; humeri moderately rounded, slightly narrowed; striae entire, slightly impressed, very finely punctate on disk; 3rd interval with 11 or 12 (over entire length), 1st with 1 or 2 (basally, outside scutellar stria), 5th with 5 or 6 (basal $\frac{1}{2}$) setigerous punctures. Inner wings full. Prosternum with a few punctures at sides anteriorly; mesosternum distinctly. metasternum less distinctly, punctate at sides; abdomen impunctate, alutaceous.

Measurements: ♀ just over 11 by 4.4. mm.

Type: Holotype ♀ (M. C. Z. no. 21, 781) unique from "Bachwng B," Lake Superior, dated "15.8" (presumably August 15), from Hubbard and Schwarz in the Leconte Collection in the Museum of Comparative Zoölogy.

Distribution: Known only from the type locality. It is astonishing to find so distinct a new form from such a locality, but there is no reason to doubt the label. The genus is not very close to anything previously known even outside of America.

3. Platidius Chd.

Chaudoir 1871, p. 51.

GENOTYPE: Patrobus aterrimus Dej., by present designation (Platidius originally described for this species and P. depressus Gebler of Asia).

Platidius has been combined with Diplous Mots. (Asiatic), apparently as the result of some indecisive notes by Bates (1873, p. 295), but I prefer to follow Chaudoir until the synonymy can be settled

⁵ Spelled Bachewauung, Bachewauung, Batchawaung, and Batchawana Bay on various maps. It is a part of Whitefish Bay, eastern end of Lake Superior, Ontario, Canada.

more definitely. The genus is a natural one, related to *Patrobus* but differing in many details, the more important of which are given in the key to genera, above. The American species are mutually similar in appearance, depressed form, black color (elytra often brownish in *aterrimus*), full inner wings, and most other asexual characters, as well as in the general structure of the male copulatory organs. The males of our four species are easily separable by secondary sexual and slight genitalic characters; the females can usually be placed by the relatively slight asexual characters. All four species (I have taken them all) live in coarse gravel or among stones or under other cover beside brooks and rivers.

KEY TO AMERICAN SPECIES OF PLATIDIUS CHD.6

- 2. Inimit trochanters usually pointed, about ½ length femora (but somewhat variable); I front femora angulate or dentate; (pronotum less rugosely punctate) (western America)....... 3
- 3. Apex of phallobase (middle lobe) of genitalia truncate, with left side irregular, angulate, or hooked; apical spine of eversible sac entirely chitinized; (body slightly larger, more depressed, with intervals of elytra usually flatter and duller.)

 2. aterrimus (Dei.)
- Apex phallobase rounded, left side not angulate nor hooked; apical spine of eversible sac chitinized only at base, membranous apically; (slightly smaller, less depressed, elytral intervals usually more convex and more shining).

3. filicornis Csy.

⁶ The following species are incorrectly cited as *Platidius* (or *Diplous*) in the Leng and Junk Catalogues: *obtusiusculus* Chd., *stygicus* Chd., *angusticollis* Mann. They will be found below under *Patrobus*.

1. Platidius californicus (Mots.)

(Male genitalia, Pl. 3, figs. 80–88; range, Pl. 4, map A)

Patrobus californicus Mots. 1859, p. 123 (listed previously in

Kaefer Russl. 1850, p. 6); Lec. 1869, p. 375; Horn 1875, p.

131: Patrobus trochantericus Lec. 1869, p. 375: Platidius

californicus Csy. 1918, p. 399: latipennis Csy. 1918, p. 399:

incisus Csy. 1918, p. 399: strenuus Csy. 1918, p. 400; rectus

Csy. 1918, p. 400: sierranus Csy. 1918, p. 401: breviusculus

Csy. 1918, p. 401.

The important characteristics of this species are given in the key. The male genitalia have the apex of phallobase rounded, left side not hooked nor angulate; apical spine of eversible sac rounded-spatulate at apex, with base flatter and less trough-like than in other Platidius.

Measurements: $\gtrsim 10.5^7 - 17$ by 4.1 - 5.6; $\gtrsim 12 - 17$ by 4.3 - 5.5 mm.

Types: Californicus was described by Motschulsky from near San Francisco, California; the type(s) are probably now in the Moscow Museum; there is a \$\rightarrow\$ from Motschulsky in the Leconte Collection which may be a cotype (type no. 8,232). Leconte's trochantericus was from Fort Crook, northern California [in the upper Sacramento Valley]; the type is, of course, in the M. C. Z., no. 5,593. Casey's latipennis was from Mendocino and Humboldt Cos., California; incisus, south of San Francisco; sierranus, California (Mokelumne Hill, Calaveras Co.) and Nevada (Reno); rectus and breviusculus, Reno, Nevada; strenuus, Washington State. The Casey types are all in the U. S. N. M.; I have seen them.

Distribution: "South of San Francisco," California, to southern British Columbia, east to western Nevada and Montana. Including material borrowed, I have had 108 specimens of this species at the M. C. Z. for study, and have seen many additional elsewhere.

Discussion: There is a good deal of variation in size, development of male secondary sexual characters, exact shape of prothorax, relative lengths of segments of maxillary palpi (apical $\frac{1}{3}$ longer to scarcely longer than subapical), exact form of apex of phallobase (examined in more than 40 males) and of apical spine of eversible

⁷ Casey gives 9 mm. for the unique δ type of his *breviusculus*. This is correct for the specimen in its present position. However, with characteristic lack of discrimination, and in spite of the fact that he makes size one of the first characters in his key description of *breviusculus*, Casey fails to mention that the specimen is hunched up, and would measure at least 10.5 mm. if it were straightened.

sac (examined in several males from well scattered localities), and in some other characters, but I have been unable to divide the species into satisfactory subspecies.

2. Platidius aterrimus (Dej.)

(Male genitalia, Pl. 3, figs. 89–97; range, Pl. 4, map A) Patrobus aterrimus Dej. 1828, p. 32; Horn 1875, p. 130 (part):

Patrobus aterrimus Dej. 1828, p. 32; Hom 1873, p. 130 (part):
Patrobus fulcratus Lec. 1869, p. 374: Platidius aterrimus
Chd. 1871, p. 51; breviceps Csy. 1918, p. 402: tenuitarsis Csy.
1918, p. 403: coloradensis Csy. 1918, p. 403: reflexus Csy.
1918, p. 403.

Distinguishing characters given in key. Male genitalia with apex of phallobase truncate, left side before apex irregular, angulate, or hooked; apical spine of eversible sac rounded or pointed at tip, more or less folded or trough-like at base, entirely chitinized.

Measurements: $\bigcirc 9-12.5$ by 3.3-4.4; $\bigcirc 10-13$ by 3.6-4.5 mm.

Types: Described by Dejean from specimen(s) received from Eschscholtz, from Norfolk Straits, northwest coast of North America; type probably now in Oberthür Coll. This type locality is probably the old Norfolk Sound, near Sitka; there is a \(\varphi\) in the Leconte Collection labeled, "P. aterrimus! Sitka Esch." which may be a cotype. Leconte's fulcratus (type in M. C. Z., no. 5,594) was from Vancouver Island; all of Casey's species (types seen by me, all in U. S. N. M.), from Colorado, where no Platidius except aterrimus is known to occur. Coloradensis is more specifically from Red Cliff; breviceps, from Boulder Co.

Distribution: Southern Alaskan coast south to central Oregon, east to Edmonton, Alberta, and southeast to Colorado. Altitudinal range is from sea level on the coast to from 7,000 to 10,000 ft. in Colorado (extremes of 10 Colorado localities of which altitudes are given). I have had 178 specimens (many borrowed) at the M. C. Z. and have seen more in other museums.

Discussion: My identification of aterrimus is based upon specimens from Sitka, which is certainly very near the type locality. Besides Eschscholtz' female mentioned above, I have seen and dissected a male collected at Sitka by T. Kincaid and now in the U. S. N. M. I think that the present species is the only Platidius which occurs as far north as the Sitka region. There is a good deal of individual variation in size, in color, and in form of apex of phallobase of male genitalia. Some of the variation is indefinitely geographic—coastal specimens run smaller and blacker than those from Alberta, and coastal males usually have the apex of the phallobase

only weakly angulate on the left side, but coastal specimens can be matched in all characters by some of those from the interior, especially from Colorado and Utah. Individual variation is so great that I cannot define recognizable subspecies. Males from single localities in southern British Columbia show almost the entire range of variation of apex of the phallobase. I have examined this character in practically all the males I have had for study; the spine of the eversible sac has been examined in relatively few specimens, but from well scattered localities.

3. Platidius filicornis Csy.

(Male genitalia, Pl. 3, figs. 98–101; range, Pl. 4, map A)

Patrobus aterrimus Horn 1875, p. 130 (part): Platidius filicornis

Csy. 1918, p. 404.

Differs from aterrimus as described in key above and in discussion below. Male genitalia with apex of phallobase rounded, left side before apex oblique, not angulate nor hooked; apical spine of eversible sac irregularly rounded or spatulate at tip, more or less folded at base, strongly chitinized only at base, membranous apically.

Measurements:

8.5–11.5 by 3.2–3.9;

10–11.7 by 3.7–4.1 mm.

Type: A

from Redwood Creek, Humboldt Co., California, in U. S. N. M.; I have seen it.

Distribution: Besides the type, I have seen 40 males, 24 females, from northern California to southern British Columbia. As compared with the related aterrimus in the coastal part of its range, filicornis seems usually to occur along smaller brooks and at higher altitudes. It is characteristic of the streams on the slopes of Mt. Hood and Mt. Rainier, for instance, and sometimes ranges up nearly to the foot of the glaciers (White River Glacier and Zigzag Cañon, Mt. Hood). However, its range probably overlaps that of aterrimus, for filicornis occurs also below 1,000 ft. In several cases the two species are known from the same localities; I have males of each, well characterized by both external and genitalic characters, from Spious Creek and from mountains between Hope and Okanagan, British Columbia.

Discussion: This species averages smaller than aterrimus, slightly more convex, with elytral intervals almost always more convex, although there is some variation in both species. Individual variation in form of prothorax, presence or absence of carinae in basal angles, development of male secondary sexual characters, and in some other details is much greater within each species than any difference between the two. I consider filicornis a species rather than a sub-

species of aterrimus because the two remain distinct even where their gross ranges overlap. In filicornis as in aterrimus I have examined the apex of the phallobase in practically every male specimen I have seen. I have dissected out the spine of the eversible sac in only a few specimens, but from well distributed localities.

4. Platidius rugicollis (Rand.)

(Male genitalia, Pl. 1, fig. 1; Pl. 3, figs. 77–79)

Patrobus angicollis Rand. 1838, p. 1 (misprint): rugicollis Rand. 1838, p. 560 (list errata); Horn 1875, p. 130: Patrobus longipalpus Notman 1919, p. 231.

Sufficiently defined in key. Male genitalia with apex of phallobase rounded, left side not angulate nor hooked; apical spine of eversible sac more or less pointed at tip, folded at base, entirely chitinized.

Measurements: 3.7-4.0; 9.5-12.0 by 3.5-4.2 mm.

Types: Randall's type, from Hallowell, Maine, is probably lost; I here designate as neotype a male from Grafton Notch, near Bethel, Maine, collected by Dr. J. G. Gehring (type no., M. C. Z. 23,357). Notman's type, a ♀ from Keene Heights, Essex Co., New York, is in Mr. Notman's collection, where I have seen it.

Distribution: Northeastern North America. I have seen a good series from Nova Scotia (Port-au-Pique) and "Canada," Maine (Bethel), Vermont (Clarendon), New Hampshire (various localities in the White Mts.), New York (including Adirondack and Catskill Mts.), and "Pennsylvania." In the White Mts. the species is usually found locally beside large streams in the "notches" or at the foot of the larger mountains, at 1,000 or 2,000 ft. altitude. It has been recorded also from the summit of Mt. Washington, but is certainly not established there.

Discussion: The proportions of the segments of the maxillary palpi (apical $\frac{1}{2}$ longer than subapical) used by Notman to distinguish his species from rugicollis (apical segment relatively shorter) are within the range of variation of rugicollis from New Hampshire. I have no doubt of the synonymy.

4. Patrobus Dej.

Dejean 1821, p. 10.

Genotype: Carabus atrorufus Stroem.8

This genus is sufficiently defined in my generic key; for a bibliog-

⁸ The name *Patrobus* was first proposed by Megerle in correspondence. So far as I can find, however (and Dr. Walther Horn 152

raphy of the genus see the *Junk Catalogue*, Vol. 2, p. 337 (Pars 98, by E. Csiki, 1928). The following is not a definition of the genus but a discussion (for the American species) of some characters which can be disposed of more economically by generalities than by repetition under the species.

Form, including degree of ventricosity, often variable, usually not dependable in classification; surface of head and pronotum always nearly smooth and shining (except as punctate in impressions or foveae), that of elytra finely alutaceous. Under high power the alutaceous micro-sculpture of the elytra is seen to consist of very fine reticulations which are strongly transverse in longicornis, more weakly or not transverse in other species. Head: eyes moderately prominent, but sometimes variable in individuals; front between eyes not or slightly transversely impressed (variation individual in all species); basal transverse constriction deep, more or less punctate; antennae uniform in general structure, variable in stoutness in different species (third segment 4 or more times long as wide in longicornis, between 2 and 3 times in foveocollis, intermediate in other species); maxillary palpi slender, apical segment longer

has very kindly checked this for me), the name was not published until it was listed in the "Catalogue de la Collection des Coléoptères de M. le Baron Dejean," 1821, p. 10. Five species were listed under Patrobus in this catalogue: rufipes [Fab.], excavatus Payk., foveicollis Esch., rufipennis Hoff., and americanus Dej. The last three were at that time unpublished manuscript names, but the first two were previously described species, and their citation validates Patrobus Dej., 1821. One of these two previously described species must be taken as the genotype of *Patrobus*, and Curtis (1827, p. 192) has fixed the genotype as the first, Carabus rufipes Fab. this would be simple enough except that Carabus rufipes Fab. turns out to have been misidentified by Dejean and Curtis and to be not what we call *Patrobus* at all, but a species of *Calathus*. Nevertheless, Patrobus has invariably been applied to the insects now known by that name, and its meaning ought not to be changed by a technicality. I shall, therefore, follow Curtis and Andrewes (1935) in considering as the genotype of Patrobus the insect which Dejean and Curtis incorrectly called Carabus rufipes Fab., which is the insect now known as Patrobus atrorufus (Stroem). If this is not quite in accord with the rules for fixation of genotypes set forth by the International Committee on Zoölogical Nomenclature, it is to be hoped that a suspension of the rules may be obtained and the name Patrobus preserved in the sense in which it has always been used.

than subapical ($\frac{1}{4}$ or less longer in longicornis, about $\frac{1}{2}$ longer in other species); frontal foveae moderate, except subobsolete in foveocollis; sides of neck below punctate; single coarse gular puncture (concealed by prosternum if head depressed) present, except usually absent in septentrionis. Prothorax cordate or subcordate, often individually variable; median groove of pronotum very coarse basally; basal foyeae large, deep, punctate; punctation of anterior transverse impression variable, as described for species below; basal angles finely carinate; lateral margins narrow (narrowest in foveocollis). Elutra with humeri always moderately prominent (never so narrowed as in some European species); striae entire, except usually obsolete at extreme apex in foveocollis, slightly impressed on disk (most impressed in *longicornis*), rather finely punctate (most coarsely so in longicornis); outer edge each third interval 3-punctate, rarely 4-punctate. Inner wings (Pl. 1, figs. 10–17) full, vestigial, or simply and asexually dimorphic; when vestigial, wing is narrow, strap-shaped, unfolded, reaching to or beyond middle of elytra in all species except longicornis, in which Punctation of prosternum varies vestiges are much shorter. as described in species below; meso-, metasternum, and first ventral more or less lightly punctate at sides; abdomen otherwise impunctate, alutaceous; metepisterna always elongate, never so shortened as in some European species; last ventral segment with apex not or slightly emarginate; 10 legs uniform in general structure, most slender in longicornis, stoutest in Males slightly smaller and slightly narrower foveocollis. (average) than females; anterior femora slightly stouter; first two segments each front tarsus moderately dilated, biseriately squammulose; 1 submarginal puncture each side last ventral (2 in 9); copulatory organs as described and figured, varying as described in following key.

¹⁰ In *longicornis*, *lecontei*, and *fossifrons* the last ventral is usually emarginate, uncommonly not (both sexes); in *septentrionis* the reverse is true; in *foveocollis* the last ventral seems always to

be entire.

⁹ There are 4 setigerous punctures on the left, 3 on the right third interval in Leconte's type of rufipes (=lecontei); 4 on each side in a specimen of foveocollis from Russian America, although 3 is the normal number in the species. There are several published records of 4-punctate Patrobus; such individuals are probably to be expected occasionally in all species.

KEY TO AMERICAN¹¹ SUBGENERA AND SPECIES OF PATROBUS¹²

1. Anterior transverse impression of pronotum, and middle of prosternum anteriorly, without distinct coarse punctures; (3 genitalia with phallobase angulate, denticulate, or hooked on left side near apex; eversible sac twisted to left when within phallobase, long; apical plate moderate; accessory spine single, simple, deeply withdrawn into phallobase, not hinged to latter).....................(Neopatrobus subgen. n.) 2

¹¹ A key to the European species of *Patrobus*, which are distinguished by very different characters from the American ones, has been published by Roubal and Schauberger (1928, p. 86). All the European species (about 5, all seen by me) belong to *Patrobus s. s.* and are closely related to *septentrionis*.

¹² Besides the living *Patrobus*, the following four fossil species have been described from the Pleistocene interglacial deposits of

Ontario and Illinois.

Patrobus gelatus Scudder (1890, p. 530, Pl. 1, fig. 48) from the interglacial clays of Scarboro, Ontario. Known from a single pronotum (the type) in good condition, Scudder number 14,586, now in the M. C. Z. I have examined this specimen and find it represents a species extremely close to and possibly identical with the living Patrobus fossifrons stygicus Chd. which is widely distributed

in northeastern North America to-day.

Patrobus decessus Scudder (1900, p. 73, Pl. 7, fig. 4) from interglacial deposits at Reservoir Park (Toronto) and Scarboro, Ontario. Known from 10 elytra: the type (by present designation) is the specimen figured by Scudder (his number 16,782), now in the M. C. Z. This species was supposed by Scudder to be related to the living Patrobus (= Platidius) rugicollis Rand. However, I have examined the fossil type and find that the humerus is formed as in typical Patrobus, much less prominent than in Platidius, and various details of sculpture (including the presence of a conspicuous ocellate puncture at base of elytron between the first and scutellar striae) show that this fossil species, like the preceding, was really similar to the living Patrobus fossifrons stygicus.

Patrobus frigidus Scudder (1900, p. 74, Pl. 7, fig. 6), also from Reservoir Park, Toronto. The type is a single elytron, Scudder number 16,793, and is in the M. C. Z. It is distorted, but is certainly a true Patrobus, not related to Platidius rugicollis as supposed by Scudder, and is in all probability the same species as the preceding. The profuse red speckling of the elytron is probably not

natural but due to some accident of preservation.

Patrobus henshawi Wickham (1917, p. 140, no fig.) from the interglacial Sangamon Peat near Mahomet, Illinois. Known from the head, prothorax, and part of an elytron of one individual, the

- This impression shallow and poorly defined ______3

- 4. Frontal foveae normal; wings full; 16 (apex of phallobase beyond orifice short, not strongly sinuate; eversible sac not twisted when within phallobase, short; apical plate short; accessory spine single but with dilated base, hinged to phallo-

type, formerly in the museum of the University of Illinois, but said now to be lost. I can say nothing about the true relationships of the species. It comes from about the same horizon as Scudder's species and is about the same size.

In my opinion, Scudder's three fossil *Patrobus* are all based on fragments of a single species which was very similar to, and perhaps the same as, the living *P. fossifrons stygicus*. The true position of Wickham's species is unknown. I therefore propose the following tentative synonymy of North American fossil *Patrobus*:

1. Patrobus gelatus Scudder

(decessus Scudder) (frigidus Scudder) (? fossifrons stygicus Chd. (Recent))

2. (?) Patrobus henshawi Wickham

¹³ In American septentrionis the front of the pronotum in the region of the anterior transverse impression is usually rather closely punctate, the middle of the prosternum anteriorly often less so; in foveocollis the front of the pronotum is rarely almost impunctate, but the middle of the prosternum anteriorly is almost always conspicuously punctate. The punctation character used in the key is not quite infallible, but it fails in probably less than 1% of American specimens of Patrobus.

¹⁴ In some European relatives of septentrionis (Patrobus s. s.)

the phallobase is angulate or hooked on left side at apex.

¹⁵ The relative widths of head and of base of prothorax do not quite always separate *fossifrons* and *lecontei*—rare individuals of both species are intermediate—but the measurements are very helpful in most cases.

¹⁶ In some European relatives of *septentrionis* (*Patrobus s. s.*) the wings are vestigial.

base by a lightly chitinized plate visible only when sac is everted, never deeply withdrawn into phallobase) (Patrobus s. s.).........................4. septentrionis Dej.

Genotypes of Subgenera: for Neopatrobus, longicornis as here defined; for Geopatrobus, foveocollis as here defined; for Patrobus s. s., same as for genus (the genotype, atrorufus Stroem, has the male genitalia almost identical in general structure with those of septentrionis).

The essential characters of the subgenera are in the armament of the eversible sac of the male genitalia. They can be seen most clearly in Pl. 1, figs. 2–4.

1. Patrobus (Neopatrobus) longicornis (Say)

(Wings, Pl. 1, figs. 11–12; male genitalia, Pl 2, figs. 18–27; range, Pl. 5, map C)

Feronia longicornis Say 1825, p. 40; 1859, p. 466: Patrobus americanus Dej. 1828, p. 34: Patrobus longicornis Chd. 1871, p. 48; Horn 1875, p. 130; Schaupp 1882, p. 56; 1882a, Pl. 1, figs. 2, 2a-d; Blatchley 1910, p. 87, fig. 55; Csy. 1918, p. 395; Darl. 1936, p. 143, Pl. 1, figs. 12a, b.

Description: Rather broad, elytra rather broadly oval, not distinctly ventricose; body black or piceous, legs rufous to testaceous; head and pronotum exceptionally shining. Head $\frac{4}{5}$ (slightly \pm) width prothorax; frontal sulei normal, impunctate; basal constriction slightly or not distinctly punctate at bottom; antennae of maximum length for genus, 3rd segment 4 or more times long as wide; maxillary palpi long, but apical segment only $\frac{1}{4}$ or less longer than subapical. Prothorax cordate, $\frac{1}{3}$ (slightly \pm) wider than long; base slightly narrower than head; sides more or less strongly sinuate before right or slightly obtuse basal angles; anterior impression very deep, groove-like, impunctate. Elytra $\frac{3}{7}$ (\pm) wider than prothorax; humeri broadly rounded but not much narrowed; striae more impressed and more coarsely punctate than in other species; intervals finely, strongly transversely alutaceous. Inner wings

dimorphic, vestigial form shorter than in other species. Prosternum punctate only at sides anteriorly. Legs of maximum slenderness for genus. Male copulatory organs as described in key above; phallobase relatively longer than in other *Neopatrobus*, with subapical tooth or angulation submarginal rather than marginal; eversible sac with variable dark spot beside accessory spine, caused by a scaly thickening and patch of bristles.

Measurements: \circlearrowleft 9.2 (exceptional)-13 by 3.3-5.0; \circlearrowleft 10.6-14.3 by 4.2-5.4 mm.

Types: Say's type locality is not exactly specified, nor is Dejean's, but their specimens probably came from eastern United States. Say's type is probably lost; Dejean's should be in the Oberthür Collection. To replace Say's type I have labeled and here designate as neotype of Patrobus longicornis (Say) a ♂ from Arlington, Mass., type no. 22,982 in the M. C. Z.

Distribution: Newfoundland (several localities in south and west) to southern British Columbia (many localities, but none quite coastal), south to Florida (Jacksonville) and Arizona (foot of Pinal Mts.). Not at high altitudes (probably not regularly above 2,000 ft.) in either the White or Appalachian Mts.; four Colorado localities with definite altitudes range from 4,800 to 8,000 ft., which is low for that region. The species is already known from every province of southern Canada and it is not unlikely that it occurs in some part of every one of the United States, being absent only in a narrow coastal strip around the Gulf of Mexico and in a small area in the south and southwest. It is not yet recorded, however, from California, Nevada, Louisiana, Mississippi, nor Alabama. Common; usually under cover (by day) on the upper banks of rivers or ponds, or in damp woods away from water.

Discussion: A distinct and universally recognized species, although not so isolated phylogenetically as some of the species lumped by Horn under septentrionis. Unique in appearance, slenderness of appendages, depth of anterior pronotal impression, depth of elytral striae and coarseness of strial punctures, strongly transverse elytral microsculpture, small size of vestigial wings in short winged individuals, minor details of male genitalia, and temperate rather than arctic or subarctic distribution. There is no significant geographical variation in size, although Colorado specimens run rather small. In southeastern specimens the basal angles of the prothorax tend to be a little more prominent than usual, but the difference is slight and inconstant. As I have shown recently

(1936, p. 143), the wings are vestigial in more than 90% of individuals, but fully winged specimens (about 9%) occur probably throughout the species' range. (See also Pl. 5, map C, below.) In the male genitalia the apex of the phallobase (examined in about 60 specimens) varies geographically; northern and western specimens have the apex strongly toothed about as in Pl. 2, figs. 20 or 23, but with some variation; males from central New England to Iowa have it about rectangularly, but also somewhat variably, denticulate or angulate; those from the southeast have it obtusely and inconspicuously angulate (fig. 26). The transition is gradual, however, and variation prevents the separation of distinct subspecies. On the whole, and in spite of what has just been said, there is distinctly less individual variation in this species than in any of those which follow.

2. Patrobus (Neopatrobus) lecontei Chd.

(Wings, Pl. 1, figs. 13–14; male genitalia, Pl. 2, figs. 28–37; range, Pl. 5, map C)

(a) P. l. lecontei Chd.

Patrobus rufipes Lec. 1863, p. 18 (not Duft.): lecontei Chd. 1871, p. 47 (part): septentrionis Horn 1875, p. 130, and others (part): canadensis Csy. 1924, p. 67.

(b) P. l. gravidus subsp. n.

Patrobus lecontei Chd., l. c. (part).

Description (species as a whole): Form average, not distinctly ventricose except in extreme females; black or piceous, legs rufous to testaceous. Head \(\frac{3}{4}\) or slightly less width prothorax; frontal sulci normal, with bottoms somewhat irregular but not distinctly punctate; basal constriction slightly punctate at bottom. Prothorax relatively large, $\frac{1}{3}$ (slightly \pm) wider than long; base slightly wider than head; sides arcuate anteriorly, usually only slightly or faintly sinuate before nearly right or slightly obtuse basal angles; anterior transverse impression shallow, indefinite, usually impunctate, rarely with slight fine punctation. Elytra $\frac{3}{7}$ wider than prothorax in ventricose females, slightly narrower in other specimens; humeri broadly rounded but not much narrowed except in ventricose females. Inner wings dimorphic. Prosternum obsoletely punctate, but only at sides anteriorly. Male copulatory organs as described for subgenus; scarcely distinguishable from some fossifrons (especially subsp. dimorphicus) except that accessory spine of eversible sac is twisted in lecontei and not in fossifrons; sac without dark spot in specimens examined.

2a. P. (N.) lecontei lecontei Chd.

Average size smaller; basal foveae of prothorax less punctate; elytra slightly less dull in female. Wings dimorphic: vestigial in about \(^3_4\) or more of individuals, full in \(^4_4\) or less.

Measurements: 27 33 8.5–10.8 by 3.2–4.0; 25 9 9.5–11.5 by 3.7–4.2 mm.

Types: Patrobus lecontei is expressly stated by Chaudoir to be a new name for the preoccupied rufipes Lec. Leconte's type (M. C. Z. no. 5,592) is a ♀ from the North Red River (southern Manitoba or the Minnesota-Dakota line), and this must be considered the type locality of lecontei in spite of the fact that Chaudoir's specimens were from Newfoundland. Casey's types (U. S. N. M.) were from Edmonton, Alberta; I have seen them.

Distribution: Typical lecontei occurs in the north-central region, from Colorado (Gunnison, 7,500; Poncha Springs, 7,400 ft.) to Alberta (Edmonton and other localities), western Lake Superior, and "Hudson Bay." Mr. J. B. Wallis writes that specimens of lecontei which he took at Roche Percee, Saskatchewan, were under logs and other cover near ponds, often in company with Dytiscus pupae.

2b. P. (N.) lecontei gravidus subsp. n.

Larger than typical *lecontei*; basal foveae of prothorax a little more closely and coarsely punctate; elytra slightly duller in female. Wings vestigial in all specimens seen.

Measurements: $5 \circlearrowleft 10.2-11.2$ by 3.8-4.2; $2 \circlearrowleft 11.5-12.5$ by 4.5-4.7 mm. (Chaudoir: both sexes, 11-12 mm.).

Types and distribution: Newfoundland, holotype ♂ (M. C. Z. no. 21,782) and 4 ♂♂, 2 ♀♀ paratypes (M. C. Z., 1 ♂ in Canadian National Collection) all from Little River, southwest Newfoundland, July 10–18, 1905 & 1907, collected by the late Percy Gardner Bolster. Chaudoir's specimens were from St. Pierre Island, south coast of Newfoundland.

Discussion: The relationship of lecontei (both subspecies) and fossifrons (below) is closer than that of any two other American Patrobus. The color of the legs is diagnostic in clean, mature specimens. Upon comparison, lecontei is seen to be a distinctly stouter species, with relatively narrower head and more ample prothorax, the sides of which are usually less sinuate before the base. The form of the tip of the phallobase in lecontei males is almost exactly like that of Patrobus fossifrons dimorphicus of western North America, but is much less barbed than in fossifrons stygicus, the subspecies

of fossifrons with which lecontei occurs over most of its range except Colorado. The size difference between the two subspecies of lecontei is, on an average, more than 10% of the total length in each sex, but extremes of the two subspecies overlap in size. The other characters are of minimum subspecific value in this variable genus.

- 3. Patrobus (Neopatrobus) fossifrons (Esch.)
 (Wings, Pl. 1, figs. 15–16; male genitalia, Pl. 1, fig. 2 & Pl. 2, figs. 38–54; range, Pl. 5, map C)
- (a) P. f. fossifrons (Esch.)

 Platysma fossifrons Esch. 1823, p. 104; Fisch. 1823, p. 128, Pl.

 19, fig. 4: Patrobus fossifrons Mann. 1843, p. 194 (not Dej.
 1828, p. 31; not Chd. 1871, p. 44): longiventris Mann. 1853,
 p. 145: fulvus Mann, 1853, p. 145: latiusculus Chd. 1871, p.
 46: septentrionis Horn 1875, p. 130, and others (part).
- (b) P. f. dimorphicus subsp. n.
 Patrobus latiusculus Chd. 1871, p. 46 (part): septentrionis Horn
 1875, p. 130, and others (part).
- (c) P. f. stygicus Chd.

 Patrobus stygicus Chd. 1871, p. 46: septentrionis Horn 1875, p. 130, and others (part): tenuis Csy. 1920, p. 186 (not Lec., not Csy. 1918, p. 396).

Description (species as a whole): Form average to slender, sometimes distinctly ventricose in female, sometimes not; black or piceous, rufo-piceous below, legs not or not much paler. $Head = \frac{5}{6}$ (slightly \pm) width prothorax; frontal sulci normal, usually impunctate; basal constriction finely punctate at bottom. Prothorax rather variable, $\frac{1}{4}$ to $\frac{2}{5}$ wider than long; base as wide as or slightly narrower, or rarely wider, than head; sides arcuate anteriorly, broadly but usually not strongly (sometimes scarcely) sinuate before right or slightly obtuse posterior angles; anterior transverse impression shallow or obliterated, usually impunctate, rarely with some fine punctation. Elytra $\frac{1}{2}$ (considerably \pm) wider than prothorax; humeri moderately rounded, not much narrowed except in ventricose females. Prosternum below with sides anteriorly (almost entire sides in some individuals) more or less superficially and finely punctate. Male copulatory organs as described for subgenus; dark spot beside accessory spine of eversible sac variable, sometimes nearly absent.

3a. P. (N.) fossifrons fossifrons (Esch.)

Of maximum size and stoutness for species, with prothorax of about maximum width. Wings uniformly vestigial in all specimens (about 60) seen. Male with phallobase usually only obtusely angulate on left side near apex.

Measurements: (Unalaska) 3 10–11 by 3.6–3.9; 1 10.3–11 by 3.9–4.2 mm.: (Kodiak Is.) 3 9.5–10.7; 1 10–10.7 mm. (One smaller male seen from Kodiak Is.)

Types: Eschscholtz described fossifrons from Unalaska Island and Kamchatka; I here designate Unalaska the type locality; the types should be in the Moscow Museum. Mannerheim described both longiventris and fulvus from Kodiak Island; the types should be at the University of Helsingfors, or possibly with Chaudoir's specimens in the Oberthür Collection; there is a probable cotype of longiventris from Mannerheim in the Leconte Collection (M. C. Z. no. 5,591). Chaudoir's latiusculus was from Kodiak Island and Oregon; I here designate Kodiak Island as the type locality; the types should be in the Oberthür Collection.

Distribution: Islands of the Bering Sea and adjacent regions, and Kodiak Island. Seen by me from Unalaska $(19 \, \text{Ce})$, $19 \, \text{Ce}$, most collected by Dr. E. C. Van Dyke), Kodiak Is. $(16 \, \text{Ce})$, $7 \, \text{Ce}$, from various sources), St. Paul's Is. in the Pribilof group $(1 \, \text{Ce})$, and R(ussian) A(merica) (several specimens); the species is recorded also from Kamchatka in Asia. Dr. Van Dyke writes that his Unalaskan fossifrons were generally taken in old, dried up ponds or bogs, as contrasted with the higher and somewhat less water saturated habitat of foveocollis.

Discussion: The works of Eschscholtz and Fischer appeared in the same year, each referring to the other, but Fischer's description is quoted from Eschscholtz, who is to be considered the authority. The original description is good, and I can find no justification for Chaudoir's statement that Fischer's description applies partly to some other species. Dejean's fossifrons is, according to the very definite description, Eschscholtz' foveocollis; Chaudoir's fossifrons is equally unmistakably septentrionis. The fact that all three of these species occur on Unalaska probably led to the confusion. Manner-heim apparently recognized fossifrons correctly, but described longiventris and fulvus on differences of no taxonomic importance. Chaudoir, misidentifying fossifrons and overlooking the name longiventris, renamed the species latiusculus because it seemed to him that fulvus, based on an immature specimen, was not appropriate!

3b. P. (N.) fossifrons dimorphicus subsp. n.

Very variable in size and form. Specimens from the Pacific coastal region run smaller than typical fossifrons. from Utah, Colorado, and Idaho are as large as or rarely even slightly larger than typical fossifrons, but frequently have the prothorax narrower. Wings are vestigial in about \(\frac{3}{4}\), full in about \(\frac{1}{4}\) of individuals; the fully winged as well as the vestigial form occurs probably throughout the range of the subspecies (Pl. 5, map C), in every region from which adequate series have been seen. The vestigial wings are unusually variable in this subspecies, varying from somewhat smaller to considerably larger than the example figured (Pl. 1, fig. 15). In male genitalia the phallobase varies from obtusely to acutely angulate on left side near apex, more or less bridging the gap between the obtuse angulation of true fossifrons and the very acute barb of the following subspecies (stygicus), but usually nearer the former.

Measurements: \$\mathref{\partial}\$ 8.3–10.5 by 3.0–3.7; \$\mathref{\partial}\$ 9–11.5 by 3.2–4.3 mm. Types: Holotype \$\mathref{\partial}\$ (M. C. Z. no. 22, 983) and 12 paratypes (in M. C. Z., Canadian National Coll., and my own collection) from near Victoria, Vancouver Island, British Columbia; collected by myself Aug. 11, 1927. Also 6 paratypes from the same locality from the Hubbard and Schwarz Collection in the U. S. N. M., and 1 from the same locality in the F. S. Carr Collection. The holotype has full wings, but some other specimens of the type lot have vestigial wings. Because of the variability of this subspecies, I have confined the type series to specimens from a single locality.

Distribution: South coast of Alaska to northern California (Tallac, Bridgeport, and Eagle L.), east to Colorado (Ouray, 7,500–8,000; Hesperus, 8,300 ft.). I have seen more than 160 specimens; the species is especially common in southern British Columbia. The specimens (types) which I found near Victoria were in coarse gravel and among stones near the edge of a river.

Discussion: Under the description of latiusculus, Chaudoir made it plain that the name was to apply to Kodiak Island specimens; a single specimen from Oregon was identified with reservations, and cannot very well be designated as the type. The western mainland

¹⁷ The vestigial wings of typical fossifrons are more constant, and are usually about the size of the smallest wing vestiges found in dimorphicus, but individual variation in the latter is so great that the size of the wing vestige can hardly be used as a subspecific character.

subspecies of fossifrons, therefore, has been without a name until now. This variable subspecies would not be worth separating from typical fossifrons except for the state of the wings. However, the existence of a considerable proportion of fully winged individuals on the mainland and the apparent complete absence of such individuals on the islands seems to me sufficiently interesting and important to justify the separation, even though no single character can be depended upon to distinguish every individual.

3c. P. (N.) fossifrons stygicus Chd.

Form, as compared with subspecies dimorphicus, usually slightly more slender and less often ventricose. Wings always full. Male genitalia with apex of phallobase produced, strongly and acutely barbed or hooked on left side near apex.

Measurements: $3 \cdot 8.3-11.1$ by 3.0-3.9; $9 \cdot 9-12$ by 3.4-4.4 mm. Type: Chaudoir's type was from the south side of Newfoundland, and should be in the Oberthür Collection. Casey's specimens

of "tenuis" (1920) were from Marquette, Michigan.

Distribution: Boreal America from the interior of Alaska ("?nr. Ruby?") to the coast of Labrador and Newfoundland; south to extreme southeastern British Columbia, southern Alberta and Manitoba, and Lake Superior; not in the mountains of New England; limit of range in north unknown. Mr. W. J. Brown writes that the large series of specimens which he collected along the north shore of the Gulf of St. Lawrence were, "Under drift on the seashore and under old boards resting on moss covered rocks near the houses of the fishermen. The country is granitic rock covered in part by moss, Empetrum, etc., with no trees except stunted spruce and willows in protected places."

Discussion: The ranges of this subspecies and of fossifrons dimorphicus are essentially complementary, but there is some intergradation (or possibly overlapping) in southern British Columbia and Alberta. For example, I have seen two female specimens from as far east as Crow's Nest, southwestern Alberta (F. S. Carr Coll.) which look like dimorphicus and have the wings vestigial, and a winged male from Cypress Hills, north of Medicine Hat, Alberta (also Carr Coll.) has the left side of apex of phallobase only rectangularly angulate like dimorphicus, although another winged male from the same locality has the phallobase acutely barbed. On the other hand, I have examined 5 males, 10 females from Copper Mt., southern British Columbia (collected by Mr. G. Stace Smith, one labeled "meadow; 4,300 ft.") which are typical stygicus in form of male phallobase and which are fully winged except that one female

has vestigial wings. Copper Mt. is well within the gross range of dimorphicus. Whether stygicus and dimorphicus are really subspecies as I suppose, or whether they are closely related full species, is very hard to decide from museum specimens. Perhaps field observation of the behavior and habitat of the insects will settle the matter eventually. The possibility that mutation and dimorphism occur in the genitalia of these forms has been discussed earlier in this paper. The wings are full in every one of the 93 specimens of stygicus which I have examined—this is not including the doubtful series from Copper Mt., of course. Specimens of stygicus from Newfoundland (11 $\Im \Im$, 6 \Im) average larger than those from the mainland, even than those from just across the Straits of Belle Isle (17 $\Im \Im$, 10 $\Im \Im$), but extremes overlap.

4. Patrobus (s. s.) septentrionis Dej.

(Wing, Pl. 1, fig. 10; male genitalia, Pl. 1, fig. 4 & Pl. 3, figs. 55-69; range, Pl. 4, map B)

? Tenebrio fossor O. Fab. 1780, p. 190 (not L.): Patrobus septentrionis Dej. 1828, p. 29; Dej. & Boisd. 1837, p. 266, Pl. 106, fig. 2; Chd. 1871, p. 43; Horn 1875, p. 130, and others (part): hyperboreus Dej. 1828, p. 30: fossifrons Chd. 1871, p. 44 (not Esch.): labradorinus Csy. 1918, p. 395: minuens Csy. 1918, p. 396: tenuis Csy. 1918, p. 396 (not Lec., not Csy. 1920): tritus Csy. 1920, p. 186.

Description: Form average, not distinctly ventricose; black, sometimes piceous or rufescent, especially on elytra; legs not distinctly paler. Head \(\frac{3}{4}\) to \(\frac{5}{6}\) width prothorax; eyes varying from very prominent to much less so; frontal sulci normal, not distinctly to (especially in large \mathfrak{P}) distinctly punctate; basal constriction moderately to strongly punctate; gular puncture usually weak or obliterated. Prothorax $\frac{1}{3}$ to $\frac{3}{7}$ wider than long; base wide as head (slightly ±); sides arcuate anteriorly, usually strongly (individually less strongly) sinuate before usually very prominent right (slightly \pm) posterior angles; anterior transverse impression indefinite, almost always conspicuously punctate, rarely only slightly or not punctate. Elytra \frac{1}{2} or somewhat less wider than prothorax; humeri moderately rounded but more prominent than usual in genus. Wings always full. Prosternum coarsely and conspicuously punctate, especially latero-basally, but almost always with some coarse punctures at middle anteriorly (I have seen no specimen with punctures lacking both at front of pronotum and at middle

of prosternum anteriorly); sides of meso- and metasterna rather variably but usually more strongly punctate than in other species. Male copulatory organs as described in key.

Measurements: 3.2-9.5 by 2.9-3.5; 9-11 by 3.2-4.0 mm.

Types: Tenebrio fossor was described from Greenland; like the rest of the O. Fabricius Collection, the type is probably no longer in existence. Dejean's types of septentrionis were from Lapland, northern Sweden, and Siberia; I here designate Lapland as the type locality; the types should be in the Oberthür Collection. P. hyperboreus Dej. was from Greenland, and also should be in the Oberthür Collection. Of Casey's species, labradorinus and minuens were from West St. Modest, Labrador; tritus, from Marquette, Michigan; the types of all are in the U. S. N. M., where I have seen them.

Distribution: Circumpolar. In America, on Islands including Unalaska; St. Paul and St. George in the Pribilof Islands; and from Alaska to Labrador and Newfoundland, south to Colorado, the Great Lakes and northern Maine (Greenville), but not in the White Mts.: northern limit of range unknown. The only Colorado locality with altitude given is Leavenworth Valley, 10-11,000 ft., but the species ranges down to sea level in the north. Widely distributed also in northern Europe and Asia. Besides 98 American specimens I have seen 3 33, 2 99 from Europe (including Lapland); several from Iceland; a pair from Greenland; and a male from Copper Island, off Kamchatka. I do not know the habits of the species in America, but in Europe it is said to occur in both northern wooded and high alpine regions, and the records suggest that it has the same range of habitat here. In Iceland it favors damp meadows below 300 meters (Lindroth 1931, p. 172).

Discussion: Tenebrio fossor, if it is a Patrobus, is probably the earliest name for this species, for the black color with fulvescent elytra and abdomen, and the presence of obvious inner wings (which are mentioned in the description) are practically diagnostic. However, the name is not available because of an earlier, different Tenebrio fossor L. The name hyperboreus Dej. is applied by Chaudoir to the form of septentrionis with rufous elytra, which he calls a variety. It is, however, no more than an individual variation. In Iceland it has been observed copulating with typical black specimens (Lindroth, l. c.). If Chaudoir's application of the name is correct, Dejean's statement that hyperboreus is apterous requires confirmation. Casey's three species are all within the rather wide range of individual variation of septentrionis. American specimens usually have the front of the pronotum more punctate and the basal angles

more prominent than European ones, although there are many exceptions. The most coarsely punctate series I have seen is from the Aleutian Islands; the least punctate specimens, oddly enough, are among a series from the neighboring Pribilof Islands; mainland specimens, however, also show nearly the whole range of variation. There is a little individual variation in the form of the apex of the phallobase and much variation in the form of the accessory spine of the eversible sac of the male genitalia. Series from single localities often have the accessory spine of a form recognizably different from that in series from other localities not very far away, but some of the variation is individual and it is quite impossible to use the spine to define useful subspecies. There is no significant geographical variation in size. The wings are full in the 98 American specimens I have examined and are said always to be full in European specimens too.

5. Patrobus (Geopatrobus) foveocollis (Esch.)

(Wing, Pl. 1, fig. 17; male genitalia, Pl. 1, fig. 3 & Pl. 3, figs. 70–76; range, Pl. 4, map B)

(a) P. (G.) foveocollis foveocollis (Esch.)

Platysma foveocollis Esch. 1823, p. 105; Fisch. 1823, p. 129, Pl. 19, fig. 5: Patrobus foveocollis Dej. 1828, p. 30; Mann. 1843, p. 194; fossifrons Dej. 1828, p. 31 (not Esch.): foveicollis Chd. 1871, p. 45 (part): septentrionis Horn 1875, p. 130, and others (part).

(b) P. (G.) foveocollis tenuis (Lec.)

Pterostichus tenuis Lec. 1850, p. 207: Patrobus angusticollis Mann. 1853, p. 146: foveicollis Chd. 1871, p. 45 (part): tenuis Chd. 1871, p. 46 (not Csy. 1918 nor 1920): ? obtusiusculus Chd. 1871, p. 43: septentrionis Horn 1875, p. 130, and others (part): laeviceps Csy. 1918, p. 397: insularis Csy. 1918, p. 397.

Description (species as a whole): Form average to slender, not or slightly ventricose, more convex than usual; dark piceous to (more commonly) rufescent to strongly rufous, legs not or slightly paler. Head $\frac{3}{4}$ to $\frac{4}{5}$ (slightly \pm) width prothorax; eyes noticeably variable in prominence; frontal sulci rather variable, relatively shallow and poorly defined, partly obliterated posteriorly, not or slightly punctate; basal constriction punctate; gular puncture distinct. Prothorax $\frac{1}{4}$ (slightly \pm) wider than long; base wide as head (slightly \pm); sides arcuate anteriorly, moderately to strongly (rarely only faintly) sinuate

before obtuse or nearly right basal angles; side margins finer than in other species; anterior transverse impression indefinite or obsolete, variably punctate, rarely almost impunctate. $Elytra_{\frac{1}{3}}$ (slightly \pm) or rarely $\frac{1}{2}$ wider than prothorax; humeri moderately rounded, slightly narrowed; striae usually briefly obliterated at extreme apex. Wings always vestigial in American specimens. Prosternum anteriorly coarsely and conspicuously punctate at sides, varying from equally to much less closely, but still usually distinctly, punctate at middle anteriorly. Legs of maximum stoutness for genus. Last ventral never emarginate at apex. Male copulatory organs as described in key.

5a. P. (G.) foveocollis foveocollis (Esch.)

Larger than following subspecies.

Measurements: $4 \circlearrowleft \circ 9.7-10$ by 3.6; $2 \circlearrowleft \circ 10.3-10.7$ by 3.7-3.9 mm. Type and distribution: Confined to Unalaska and probably other islands in the Aleutian group; the type was from Unalaska and should be in the Moscow Museum. I have seen $3 \circlearrowleft \circ 1 \hookrightarrow 1$ from Unalaska and $1 \circlearrowleft 1 \hookrightarrow 1$ labeled merely R(ussian) A(merica). Dr. Van Dyke writes that he found this species on Unalaska in the hills, in drier habitats than fossifrons.

5b. P. (G.) foveocollis tenuis (Lec.)

Smaller than the preceding.

Measurements: 3 - 9.5 by 2.9 - 3.3; 9 - 8 - 10 by 3.0 - 3.6 mm.

Types: Leconte's type is a Q from Lake Superior; it is in the M. Z. C. (no. 5,590). The type of angusticollis was from Kenai, Alaska; it should be at the University of Helsingfors. P. obtusius-culus Chd. was from Rupert Land near Hudson Bay, and should be in the Oberthür Collection. P. laeviceps Csy. was from West St.

¹⁸ All specimens (about 90) which I have seen from the continent of North America and from the American Aleutian and Pribilof Islands in the Bering Sea have the wings vestigial. However, 7 males and 3 females in the U. S. N. M. from Copper and Bering Islands at the Asiatic end of the Aleutian chain are all fully winged, although they cannot otherwise be distinguished from foveocollis tenuis Lec. of North America by either external or genitalic characters. This winged form will very likely be found to range widely in northern Asia. It is certainly entitled to rank as a distinct subspecies of foveocollis, but I do not know enough about previously described Asiatic Patrobus to name it.

Modest, Labrador; insularis, from St. Paul Island, Pribilof group, in the Bering Sea; the types of both are in the U. S. N. M., where I have seen them.

Distribution: Pribilof Islands and Alaska to Labrador and Newfoundland, south to Colorado and the Great Lakes, and isolated on the higher mountains of New York and New England; northern limit of range unknown. In the north the species evidently descends to sea level; on Mt. Katahdin, Maine, it occurs between 3,000 and 4,000 ft. altitude; in the White Mts., New Hampshire, usually between 4,000 and 5,000; in Colorado the two localities are both given as 10–11,000 ft. The numerous specimens which I have collected in the White Mts. were in rotten logs or under cover on the ground in forest or slightly above tree line, usually not near water.

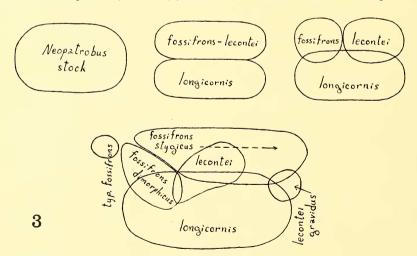
Discussion: Foveocollis was originally described by Eschscholtz as 10 mm, long. Dejean gives a slightly smaller size, but may have had a mixed series; his fossifrons (not Esch.), which is from Unalaska, 10 mm. long, is obviously from description the present species. This large form is evidently very local, for a 3 from Mt. Pavlof, Alaskan Peninsula, is scarcely over 8 mm., and a & from Atlin, northern British Columbia, is only 8.7, while the type of anausticollis from Kenai is described as 8.4. Casey's 13 specimens (types of *insularis*) from St. Paul Island, in the Pribilof group not far north of the Aleutians, also are small, 8 to 9 mm. On the eastern coast of America, specimens from Newfoundland (13, 29) are slightly larger than most mainland specimens, but not significantly so. I can find absolutely no constant character except size to separate foveocollis and tenuis; the former is really a local insular subspecies of the latter, but rules of nomenclature demand that the insular form be considered typical in this case. The citation of angusticollis as a Platidius or Diplous in the Leng and Junk Catalogues is inexplicable; the original description is reasonably good and the name has been declared a synonym of foveocollis (which it is, as a species) by Chaudoir, who had Mannerheim's type. P. obtusiusculus (type a 9 mm. 2) seems from the description to be probably an aberrant tenuis with the punctures at the front of the pronotum obliterated (as they are in two Hudson Bay specimens I have seen) and basal angles of prothorax exceptionally obtuse. Chaudoir compares the species with the European assimilis which I have seen and which is superficially very like tenuis, although it belongs to a different subgenus, Patrobus s. s. Casey's species are plain tenuis, which Casey twice misidentified.

Zoögeography of Patrobus

I should like to stress the fact that the following brief account of the history of *Patrobus* in America is only one of several possible explanations of the present distribution of the genus, but it is the one which seems to me most probable.

The present center of abundance of *Patrobus* is in Asia. All three American subgenera extend into Asia, and there are one or two additional Asiatic forms which may be entitled to subgeneric rank. Europe, in contrast, possesses only a few closely related species of a single subgenus, *Patrobus s. s.* It does not necessarily follow from this that *Patrobus* originated in Asia, but it may very well have done so. The fact that all American subgenera of *Patrobus* are primarily boreal in their distribution agrees very well with the idea that their ancestors migrated into America through the north. The Asiatic *Patrobus* fauna appears to include a larger proportion of temperate forms, although I must admit that I do not know the Asiatic fauna very thoroughly.

The ancestor of subgenus *Neopatrobus* was probably the first to reach America. After the original ancestor had spread (1), it may be guessed that (2) the original stock divided first into a boreal stock (fossifrons-lecontei) and a temperate stock (longicornis); that (3) the boreal stock then divided into a western species (fossifrons) and an eastern species (lecontei); that after the differentiation of species

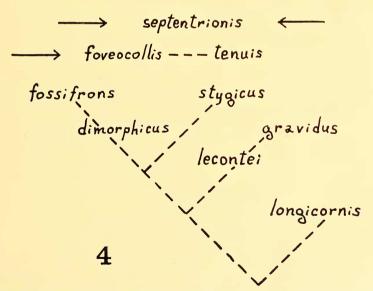


Text Fig. 3. Diagrams of four hypothetical stages in the evolution of the species and subspecies of *Neopatrobus*.

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had occurred, there was some overlapping of ranges; and that (4) finally fossifrons and lecontei set off geographical subspecies, and that subspecies fossifrons stygicus migrated eastward into and entirely across the range of lecontei. Both the fact that stygicus ranges more widely than any other Neopatrobus over recently glaciated country and the fact that it is the only form of Neopatrobus with uniformly full wings point to its being a recent migrant. Four hypothetical steps in the evolution of the species of Neopatrobus are illustrated in Text Figure 3.

Patrobus (Geopatrobus) foveocollis and P. (s. s.) septentrionis are probably relatively recent arrivals in America. Foveocollis apparently came from Asia across the region of the Bering Sea. The species has no relatives in Europe. The fact that foveocollis and its subspecies tenuis are always flightless in America and the fact that tenuis is the only one of four eastern boreal Patrobus which has isolated colonies in the mountains of New York and New England seem at first to suggest that the species is an old inhabitant, but I believe that this is incorrect. It seems to me more likely that the habitat of the species, in higher and somewhat drier places than



Text Fig. 4. Diagram to show probable origin of American Patrobus fauna. Dotted lines indicate evolution of subgenus Neopatrobus. Arrows indicate probable direction of immigration of foveocollis and septentrionis.

other *Patrobus*, accounts sufficiently both for the atrophy of the wings and for the persistence of isolated colonies on mountain slopes. Winged individuals may have disappeared recently, perhaps within the last few thousand years. Remember that specimens from islands in the western part of the Bering Sea are still winged. Winged individuals may originally have effected the spread of *tenuis* across America.

Finally, septentrionis has a circumpolar range which includes Iceland, Greenland, and islands in the Bering Sea; its closest relatives are in Europe; and it seems always to be fully winged. These facts suggest that it is a recent immigrant in America and that it may have come either from the west, or from the east, or (perhaps most likely) from both directions.

I have attempted to condense this hypothetical history of the American species of *Patrobus* into a single diagram, Text Figure 4.

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EXPLANATION OF PLATES

(All figures outlined with camera-lucida)

PLATE VI

- Fig. 1. Platidius rugicollis (Rand.). Middle lobe male genitalia: apex of phallobase, with eversible sac and apical plate extended. (Mt. Washington, N. H.)
- Fig. 2. Patrobus (Neopatrobus) fossifrons dimorphicus Darl.

 Middle lobe male genitalia, extended. (Composite:
 phallobase and eversible sac from specimen from
 Tacoma, Wash.; apical plate, from Sugar L., B. C.
 The apical plate may not be quite correctly oriented.
 I have been unable properly to evert the genitalia of
 any single specimen of Neopatrobus.)
- Fig. 3. Patrobus (Geopatrobus) foveocollis tenuis (Lec.). Middle lobe male genitalia, extended. (Mt. Garfield, N. H.)
- Fig. 4. Patrobus (s. s.) septentrionis Dej. Middle lobe male genitalia, extended. (Aleutian Islands.)
- Fig. 5. Thalassotrechus barbarae (Horn). Male genitalia, with eversible sac extended; left paramere outlined in situ, minute right paramere detached. (Sta. Barbara, Cal.)
- Fig. 6. Patroboidea rufa Van Dyke. Male genitalia: middle lobe and outline of left paramere. (Spious Cr., B. C.)
- Fig. 7. Same. Dorsal view middle lobe same individual.
- Fig. 8. Same. External characters same individual.
- Fig. 9. Platypatrobus lacustris Darl. External characters. (Female, type.)
- Fig. 10. Patrobus septentrionis Dej. Left wing. (Male, W. St. Modest, Lab.)
- Fig. 11. Patrobus longicornis (Say). Vestigial wing, with outline of hind body and right elytron. (Male, Arlington, Mass.)
- Fig. 12. Same. Full wing, to same scale. (Female, Arlington, Mass.)
- Fig. 13. Patrobus l. lecontei Chd. Vestigial wing. (Female, Edmonton, Alta.).
- Fig. 14. Same. Full wing to same scale. (Female, Tofield, Alta.).
- Fig. 15. Patrobus fossifrons dimorphicus Darl. Vestigial wing. (Male, Victoria, B. C.).
- Fig. 16. Same. Full wing, to same scale. (Male, Victoria, B. C.).
- Fig. 17. Patrobus foveocollis tenuis (Lec.). Vestigial wing. (Female, Mt. Washington, N. H.).

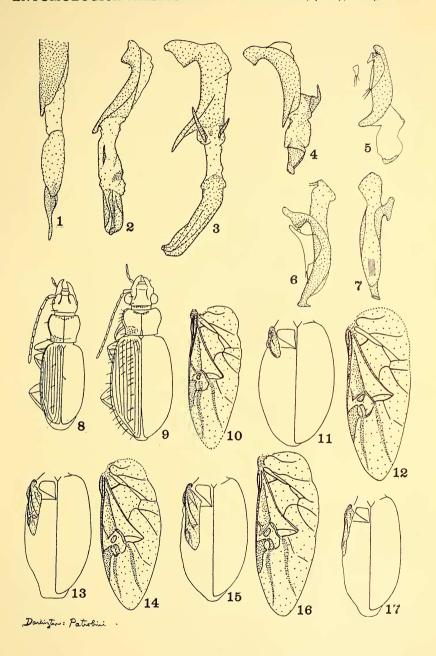


PLATE VII

- Fig. 18. Patrobus (Neopatrobus) longicornis (Say) (Edgewood, B. C.). Male genitalia from left.
- Fig. 19. Same individual. Middle lobe from above.
- Fig. 20. Same individual. Apex of phallobase from right.
- Fig. 21. Same individual. Accessory spine and pigmented area of eversible sac.
- Figs. 22–24. Same (Little R., Nfld.). Apex of phallobase from above, and from right, and accessory spine and pigmented area of eversible sac.
- Figs. 25–27. Same (Andrews, N. C.).
- Fig. 28. Patrobus (Neopatrobus) l. lecontei Chd. (Edmonton, Alta.). Male genitalia from left.
- Fig. 29. Same individual. Middle lobe from above.
- Figs. 30-32. Same (Gunnison, Col.). Apex phallobase from above, from above-right to show greatest prominence of subapical tooth, and accessory spine of eversible sac.
- Figs. 33–34. Same (type *canadensis* Csy., Edmonton, Alta.). Apex of phallobase from above, and from above-right.
- Figs. 35–37. Patrobus (N.) l. gravidus Darl. (Little R., Nfld.). Explanation as for Figs. 30–32.
- Figs. 38-41. Patrobus (Neopatrobus) fossifrons dimorphicus Darl. (West Bank, B. C.). Explanation as for Figs. 18-21.
- Figs. 42–44. Same (Yellowstone Park, Wyo.). Apex of phallobase from above, from above-right to show greatest prominence of subapical tooth, and accessory spine and pigmented area of eversible sac.
- Figs. 45–47. Patrobus (N.) f. fossifrons (Esch.) (Unalaska Island). Same explanation.
- Figs. 48–49. Patrobus (N.) f. stygicus Chd. (Copper Mt., B. C.). Apex of phallobase from above, and from above-right.
- Figs. 50-51. Same (Winnipeg, Man.).
- Figs. 52–54. Same (Flowers Cove, Nfld.). Explanation as for Figs. 42–44.

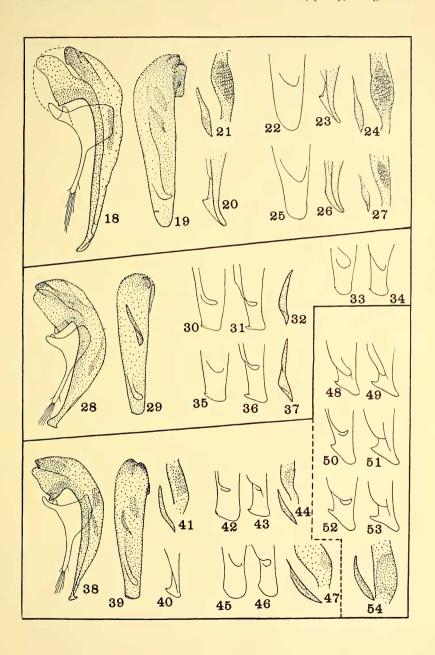


PLATE VIII

Figs. 55–57. Patrobus (s. s.) septentrionis Dej. (Aleutian Islands). Male genitalia from left, middle lobe from above, and accessory spine of eversible sac.

Figs. 58–59. Same (another individual from Aleutian Islands).

Apex of phallobase from above, and accessory spine of eversible sac.

Figs. 60–61. Same (W. St. Modest, Lab.).

Fig. 62. Same (Paroquet Is., Lab.). Accessory spine only.

Figs. 63-64. Same (Swedish Lapland).

Figs. 65–66. Same (Iceland).

Fig. 67. Same (type minuens Csy., W. St. Modest, Lab.). Apex of phallobase from above.

Fig. 68. Same (type labradorinus Csy., W. St. Modest, Lab.).

Fig. 69. Same (type tritus Csy., Marquette, Mich.).

Figs. 70–72. Patrobus (Geopatrobus) foveocollis tenuis (Lec.) (White Mts., N. H.). Male genitalia from left, middle lobe from above, and the two accessory spines of eversible sac.

Fig. 73. Same (type *laeviceps* Csy., W. St. Modest, Lab.). Apex of phallobase from above.

Fig. 74. Same (paratype insularis Csy., St. Paul Is., Bering Sea).

Figs. 75–76. Patrobus (G.) f. foveocollis (Esch.) (Russian America). Apex of phallobase from above, and the two accessory spines of eversible sac.

Figs. 77–78. Platidius rugicollis (Rand.) (Mt. Washington, N. H.).

Male genitalia from left, and apical spine of eversible sac.

Fig. 79. Same (Bethel, Me.). Apex of phallobase from above.

Fig. 80. Platidius californicus (Mots.) (Sonoma Co., Cal.). Apex of phallobase from above.

Fig. 81. Same (paratype incisus Csy., south of San Francisco, Cal.).

Fig. 82. Same (type latipennis Csy., Gualala, Calif.).

Fig. 83. Same (type rectus Csy., Reno, Nev.).

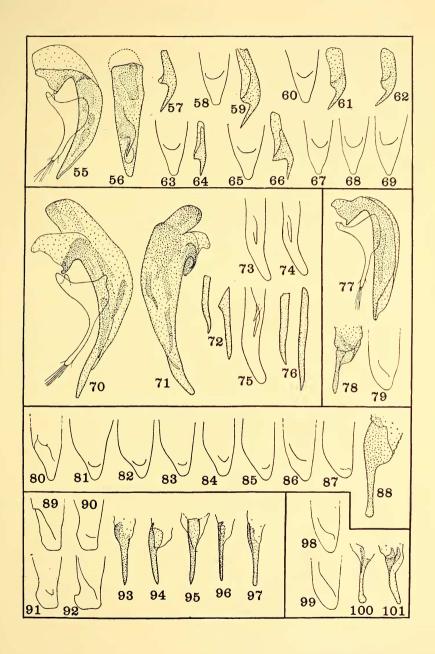
Fig. 84. Same ("californicus 4" in Casey Coll., Soda Springs, Mendocino Co., Cal.).

Fig. 85. Same (type sierranus Csy., Mokelumne Hill, Cal.).

Fig. 86. Same (Duncan, Victoria Is., B. C.).

Fig. 87. Same (type breviusculus Csy., Reno, Nev.).

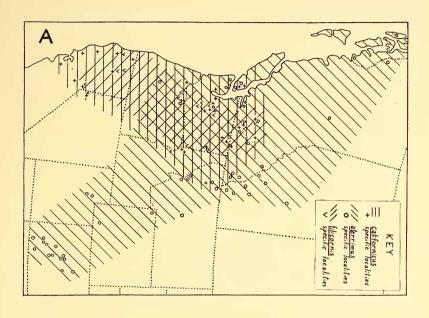
Fig. 88. Same (Indian R., B. C.). Apical spine of eversible sac.



- Fig. 89. Platidius aterrimus (Dej.) (Sitka, Alaska). Apex of phallobase from above.
- Fig. 90. Same (type tenuitarsis Csy., Colorado).
- Fig. 91. Same (type coloradensis Csy., Red Cliff, Col.).
- Fig. 92. Same (Mts. between Hope & Okanagan, B. C.
- Fig. 93. Same (Sitka, Alaska). Apical spine of eversible sac.
- Fig. 94. Same (S. Fork, San Miguel, Col.).
- Fig. 95. Same (Mts. between Hope & Okanagan, B. C.).
- Fig. 96. Same (Spokane, Wash.).
- Fig. 97. Same (N. Olympic Mts., Wash.).
- Fig. 98. Platidius filicornis Csy. (Truckee, Cal.). Apex of phallobase from above.
- Fig. 99 Same (Spious Cr., B. C.).
- Fig. 100. Same (Mts. between Hope & Okanagan, B. C.). Apical spine of eversible sac.
- Fig. 101. Same (Sisson, Cal.).

PLATE IX

- Map A. Ranges of western American species of Platidius.
- Map B. Ranges of *Patrobus* (s. s.) septentrionis Dej. and *Patrobus* (Geopatrobus) foveocollis (Esch.) in America.



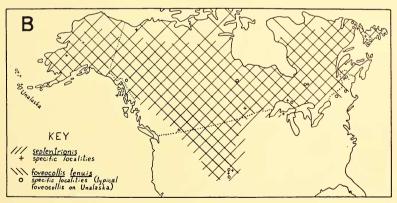


PLATE X

Map C. Ranges of species and subspecies of Patrobus, subgenus Neopatrobus, in America.